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BIOENERGETICS OF HAWAIIAN HONEYCREEPERS: THE AMAKIHI (*Loxops virens*) AND THE ANIANIAU (*L. parva*)

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TABLE OF CONTENTS

INTRODUCTION

Insular biotas have attracted considerable biological attention, and have been very important in the formulation of evolutionary thought and theory. Since Charles Darwin's visit to the Galapagos Islands and his description of the Galapagos Finches, insular land birds have played very prominent roles in evolutionary biology, largely based upon detailed morphological and taxonomic analyses.

Yet virtually no attention has been paid to assessments of the functional attributes of terrestrial birds inhabiting oceanic islands. Ideal candidates for studies of adaptive physiology of an island avifauna are the endemic Hawaiian Honeycreepers (Passeriformes: Drepanididae) which exhibit among their . . . "numerous species the most striking example of adaptive radiation from an assumed single ancestral species of any bird family in the world" (Berger, 1970). This study undertakes to examine certain bioenergetic characteristics of two congeneric species of Hawaiian Honeycreepers, the Amakihi (Loxops virens) and the Anianiau (L. parva), with the view of providing data for comparisons with those derived from continental land birds. Such data, hopefully, will reveal the magnitudes of physiological divergence and/or convergence of these island birds. Included in this study are assessments of oxygen consumption, thermoregulation, and evaporative water loss.

MATERIALS AND METHODS

The Family Drepanididae is divided into two divergent subfamilies: Drepanidinae and Psittirostrinae; Loxops is the most primitive genus of the latter subfamily (Amadon, 1950). The Amakihi (Loxops virens) is the second most common extant Honeycreeper, occurring on all of the main islands; its

broad climatic distribution suggests that it may be the most adaptable of the surviving species of Honeycreepers (Berger, 1970). Of the six L. virens employed in this study (mean initial weight: 19.2 ± 4.0 SD g), three were L. v. virens (mean initial weight: 16.8 g, range: 13.1 - 21.1 g) collected during the last week of January 1968 in the Kaohe Game Management Area on the Island of Hawaii, and at an elevation of about 7,300 ft. This is an area of mamani-naio forest, a dry, open parkland on the southern and western slopes of Mauna Kea. The three L. v. stejnegeri (mean initial weight: 21.6 g, range: 19.0 - 23.6 g) were collected on 17 May 1969 in Kokee State Park on the Island of Kauai and at elevations between 3,500 and 4,000 ft. This habitat is an ohia-koa rainforest with a mean annual rainfall of about 85 in. (Eddinger, 1970). The Anianiau (L. parva) is endemic only to Kauai where it is fairly common in the Kokee and Alakai Swamp regions of the island. Of four L. parva employed in this study (mean initial weight, 9.0 ± SD 1.0 g) some were collected in June 1969 and some in June 1970 in Kokee State Park, at the same locality as that of the Kauai Amikahi. All of the birds were collected as nestlings and then brought to the University of Hawaii, Honolulu, for hand-rearing. After fledging the birds were provided a diet of Gerber's high protein baby cereal, Deca Vi Sol babies vitamin drops, egg yolks, wheat germ, honey-water, papayas, oranges, grapefruit, apples, fly larvae, fly pupae, and autolyzed brewer's yeast fraction (see Eddinger, 1969). Except while measurements were being made, the birds were housed in large indoor aviaries, under conditions of usual room temperature and humidity, and subjected to approximately natural photoperiod. At the time of this study (July and August 1971) the birds were between 12 and 42 months of age, and all appeared to be in optimal states of health. Since the sexes of both species

are similar, no attempt was made to distinguish between them.

Body temperature (T_B) was measured to the nearest 0.1°C in each individual at the end of each measurement of oxygen consumption and after at least 1½ hr exposure to a given ambient temperature (T_A). T_B was measured either with a copper-constantan thermocouple ensheathed in plastic tubing and attached to a Leeds and Northrup portable potentiometer or a small-animal thermister attached to a Y.S.I. Telethermometer. For T_B measurements the temperature probe was inserted manually into the cloaca to a depth of at least 2 cm, and the measurement made within 30 sec after initial handling of the bird.

Ambient temperature was monitored to the nearest 0.1°C with Y.S.I. temperature probes inserted through air-tight ports into the respirometer chambers which, in turn, were contained within an insulated constant temperature cabinet equipped with refrigeration and heating units and blowers; T_A inside the respirometer chambers could be controlled to within ± 0.2°C of the desired setting. T_A was measured for each individual within 30 sec of each measurement of oxygen consumption.

Measurements of oxygen consumption were taken alternately on each of two birds placed in air-tight 3.5 l respirometer chambers equipped with ports for the introduction and removal of air and with T_A thermister probes, and placed within the darkened constant temperature cabinet. The birds rested on hardware-cloth platforms about 8 cm above the bottoms of the chambers which were covered with mineral oil to a depth of 2 cm to prevent evaporation from excreta. Air which had been dried by passage through indicating Drierite was metered to the respirometer chambers at flow rates of 800 cm^3/min and 600 cm^3/min for L. virens and L. parva, respectively. Samples of air flowing

chambers (CO_2 not removed) were then delivered to a Beckman Model E2 paramagnetic oxygen analyzer for measurements of oxygen consumption. All measurements of oxygen consumption were made on postabsorptive birds held in the dark after at least 1 hr exposure to a given T_A, and during their usual diurnal period (between 10:00 and 17:00). Measurements on each bird and at each T_A were made over a ½-hr period at 5 min intervals. The two lowest measurements for each bird at each T_A were used for calculations of oxygen consumption. Rates of oxygen consumption were corrected to S.T.P. Each bird was weighed to the nearest 0.1 g before being placed in and after removal from the respirometer chambers. Weights at the times of measurements of oxygen consumption were interpolated.

Evaporative water loss (EWL) was measured gravimetrically and simultaneously with the ½-hr measurements of oxygen consumption by passage of air effluent from the respirometer chambers through 150 mm desiccating tubes filled with small-mesh calcium chloride; this air was then delivered to the oxygen analyzer, An additional desiccating tube was used as a control to measure water vapor in the air being delivered to the respirometer chambers.

RESULTS

Body Temperature

Body temperature data for L. virens and L. parva and over a T_A range of 10 to 40°C are summarized in Fig. 1. There is a tendency toward a direct relationship between T_A and T_B, particularly at higher T_A. In L. virens the mean T_B at all T_A below 35°C is 40.3 ± SD 0.5°C (N = 18); that for L. virens from the Island of Hawaii ($\bar{X}$ = 40.4 ± SD 0.4°C, N = 9) is insignificantly higher ($p > .05$) than that for L. virens from the Island of Kauai ($\bar{X}$ = 40.1 ± SD 0.5°C, N = 9). The mean T_B of L. parva at T_A below 35°C ($\bar{X}$ = 39.5 ± SD 1.2°C,

N = 16) is significantly lower ($p < .05$) than that of L. virens collectively. At T_A = 35°C and above, both species show increasing hyperthermia with L. virens having consistently higher T_B than L. parva (Fig. 1). At T_A = 35°C the mean T_B of the six L. virens is 41.3 ± SD 0.4°C with very little difference between the island races; that for the four L. parva ($\bar{X}$ = 40.4 ± SD 0.4°C) is significantly lower, with no overlap of the range of L. virens. At a mean T_A of 39.4°C the mean T_B of five L. virens is 42.9 ± SD 0.6°C, while at $\bar{X}T_A$ = 38.3°C, that of the four L. parva is 41.7 ± SD 0.4°C.

Oxygen Consumption

The relationship between rates of oxygen consumption and T_A in L. virens is indicated in Fig. 2. At T_A < 35°C both Hawaii and Kauai L. virens showed similar responses in oxygen consumption; a line fitted by the method of least squares to these data below T_A = 35°C is described by the equation M(Metabolism) = 6.710 - 0.108 T_A. When both races are treated collectively thermal neutrality appears to extend between T_A = 30 and 35°C. The collective mean standard metabolic rate at T_A = 30°C is 3.54 ± SD 0.38 cm^3 O_2/g per hr, and that at T_A = 35°C is 3.41 ± SD 0.34 cm^3 O_2/g per hr; these means are not statistically different. When the two races of L. virens are examined separately at T_A = 35°C and above, although the sample sizes are insufficiently large for certain verification, intraspecific differences are apparent: at T_A = 35°C the three birds from Hawaii appear to be slightly above the upper critical temperature with a mean rate of oxygen consumption of 3.73 ± SD 0.45 cm^3 O_2/g per hr, while the three Kauai birds are still in thermal neutrality with a mean of 3.09 ± SD 0.17 cm^3 O_2/g per hr; sample sizes are too small for realistic tests of significance. At T_A = 39-40°C, the increase in oxygen consumption of the Hawaii race is much

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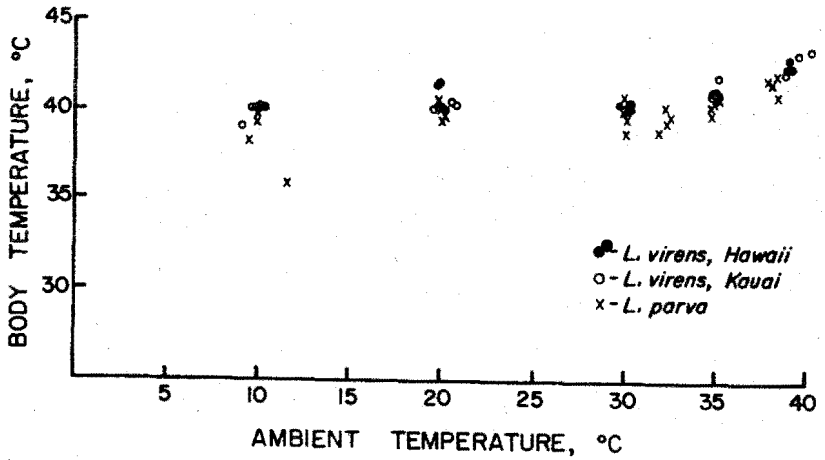

Fig. 1. The relationship between body temperature and ambient temperature in Loxops virens from Hawaii (●) and Kauai (0), and in L. parva (X).

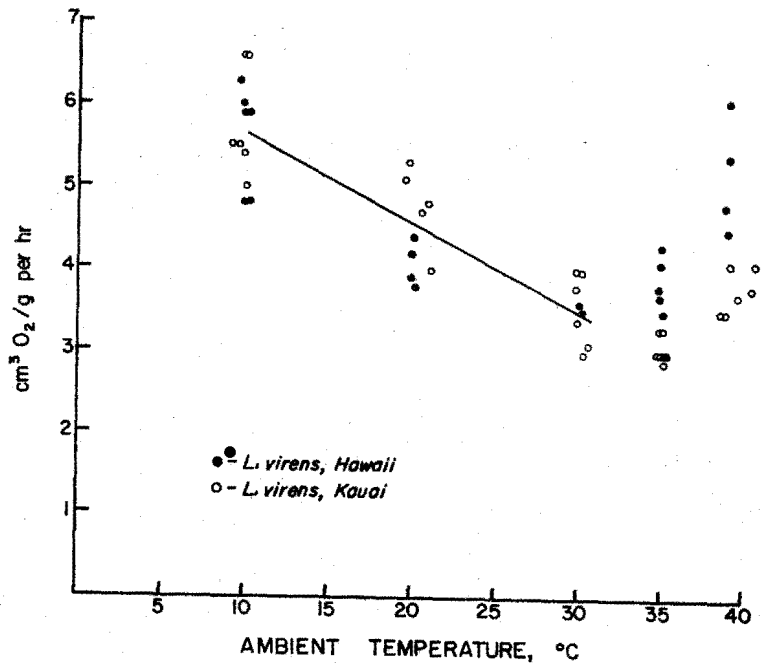

Fig. 2. The relationship between oxygen consumption and ambient temperature in Loxops virens. The diagonal line is fitted to the data below thermal neutrality by the method of least squares.

more pronounced than that of the Kauai race, with no overlap in the ranges.

The rates of oxygen consumption as a function of T_A in L. parva are summarized in Fig. 3. A line fitted by the method of least square to the data below thermal neutrality is described by the equation $M = 10.544 - .219\ T_A$. Thermal neutrality is rather sharply delineated, extending between about T_A = 31 and 36°C. The standard metabolic rate measured at $\bar{X}T_A$ = 32.4 and 35.0°C was 3.22 ± SD 0.20 and 3.23 ± SD 0.24 $cm^3\ O_2$/g per hr, respectively. This rate of L. parva (mean body weight = 7.9g) is not statistically different from the standard metabolic rate of L. virens (mean body weight = 15.3 g), in spite of nearly a two-fold difference in body weight.

Evaporative water loss

Rates of evaporative water loss (EWL) expressed both as functions of body weight and of oxygen consumption and for both L. virens and L. parva are indicated in Table 1. Expressed in both ways, there is a direct relationship between EWL and T_A; EWL increases precipitously at $T_A > 35$°C. At no T_A at which measurements of both species were made was there a significant difference between mean EWL of the two species. Assuming that 1 $cm^3\ O_2$ consumed yields 4.8 cal and that 1 mg H_2O evaporated dissipates 0.58 cal, EWL data can be used to express efficiency in heat dissipation; such an expression is included in Table 1 and indicates that at the highest T_A employed in this study only about 59 per cent of the heat produced by metabolism was dissipated by evaporative cooling in L. virens (at T_A = 39.4°C) and 54 per cent of the metabolic heat production was dissipated evaporatively by L. parva (at T_A = 38.2°C). Also included in Table 1 are estimates of atmospheric humidities of the respirometer chambers at each T_A at which oxygen comsumption, T_B and EWL were measured; relative

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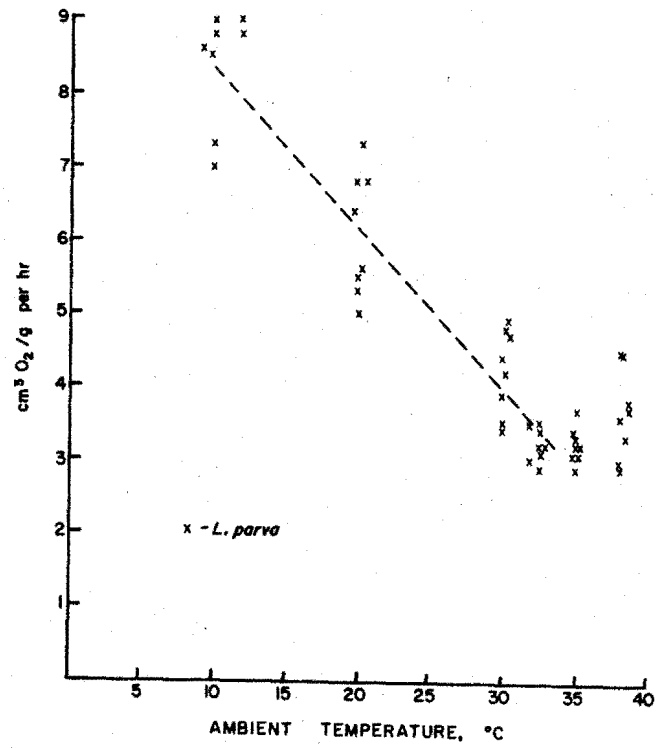

Fig. 3. The relationship between oxygen consumption and ambient temperature in Loxops parva. The diagonal line is fitted to the data below thermal neutrality by the method of least squares.

TABLE 1. Mean (± SE) rates of evaporative water loss (EWL), heat dissipation $\left(\frac{EWL}{MHP} \times 100\right)$[a], and thermal conductance (C) in Loxops virens and L. Parva, and T_A and humidities when measured.

Species	$\bar{X}$ T_A, °C	No. Animals	Evaporative Water Loss: % Body wt. / Day	Evaporative Water Loss: Mg H_2O / cm^3 O_2	Heat Dissip., % [a]	C cm^3 O_2/g/hr/°C	Atmospheric Humidity: % RH	Atmospheric Humidity: WVP, MM Hg
L. virens	9.8	6	9.1 ± 1.3	0.6 ± 0.1	7.7 ± 1.2	.189 ± .006	16.3	1.5
L. parva	9.9	3	8.3 ± 2.0	0.4 ± 0.1	4.8 ± 1.0	.302 ± .019	8.9	0.8
L. virens	20.3	6	10.1 ± 1.2	0.8 ± 0.1	9.9 ± 0.9	.220 ± .009	9.3	1.6
L. parva	20.0	4	12.9 ± 2.3	0.8 ± 0.1	9.3 ± 1.2	.305 ± .016	7.2	1.2
L. virens	30.1	6	17.8 ± 3.3	1.6 ± 0.2	18.7 ± 2.4	.348 ± .012	8.1	2.4
L. parva	30.2	4	20.7 ± 5.5	1.9 ± 0.4	22.3 ± 5.2	.412 ± .036	6.3	1.8
L. parva	32.4	4	17.8 ± 3.2	2.0 ± 0.3	23.6 ± 4.1	.442 ± .012	4.8	1.7
L. virens	35.1	6	25.1 ± 3.7	2.8 ± 0.4	33.3 ± 4.4	.551 ± .024	8.2	3.3
L. parva	35.0	4	25.8 ± 3.8	2.9 ± 0.5	35.3 ± 5.6	.594 ± .019	6.0	2.4
L. virens	39.4	5	59.8 ± 10.0	4.9 ± 0.4	59.2 ± 4.5	1.228 ± .066	15.0	7.8
L. parva	38.2	4	45.9 ± 3.7	4.4 ± 0.4	53.3 ± 4.7	1.098 ± .117	8.8	4.2

[a] Calculated assuming 1 cm^3 O_2 yields 4.8 cal and 1 mg H_2O dissipates 0.58 cal.

to follow Fig. 3

humidity was calculated after the method proposed by Lasiewski et al. (1966), and water vapor pressure (WVP) was determined from the calculated values of relative humidity.

Thermal Conductance

The mean values of thermal conductance (C), calculated from the relationship $C = M/T_B - T_A$ (where M is metabolism in cm^3 O_2/g per hr), for the two species at each T_A for which measurements are available are summarized in Table 1. In L. virens C was directly related to T_A with the mean value calculated for each T_A significantly lower than that for the next higher T_A, even below thermal neutrality. In L. parva mean C below thermal neutrality (at T_A = 10 and 20°C) was virtually constant (at .302 and .305 cm^3 O_2/g/hr/°C, respectively) and significantly higher than in L. virens. At T_A = 30°C and higher, mean C values at each T_A for which measurements were available were not significantly different between the two species, increasing directly with temperature. The greatest increase in thermal conductance for both species was between T_A of 35 and 38-39°C, in which C approximately doubled.

Tolerance to High T_A

Assuming that they could readily withstand T_A equivalent to their usual T_B (ca. 40°C), L. virens was placed in respirometer chambers for measurements at about that T_A. Of the six birds tested four died either during exposure (one bird) or after exposure (three birds) to the experimental T_A ($\bar{X}$ = 39.6°C, range 39.0 - 40.4°C). The mean T_B of the three that expired, immediately following the 1½ hr-period of exposure to high T_A, was 43.1°C (range 42.5 - 43.6°C); all expired within 36 hr following exposure. All of the birds that expired

were observed panting vigorously with beaks open while exposed to the high T_A. The two birds that survived were at T_A = 38.9 and 39.1°C; their T_B after 1½ hr exposure to high T_A were 42.2 and 43.0°C, respectively. Of these two, the one with the lower T_B was not observed panting, while that with the higher T_B panted vigorously. No differences in temperature tolerance were noted between the races of L. virens as two birds of each race perished and one survived.

After the inadvertant experience of L. virens with lethal T_A , much greater caution was taken in exposing L. parva to high T_A. The four birds were exposed for 1½ hr to $\bar{X}$ T_A = 38.3°C (range 38.0 - 38.5°C). All survived, none was observed panting, and the mean T_B immediately after exposure to high T_A was 41.7°C (range 41.0 - 42.1°C). No attempt was made to expose them to higher T_A.

DISCUSSION

The two island races of the Amakihi (Loxops virens) are considered separately in the Results section: for purposes of this discussion they will be considered collectively. When compared with bioenergetic parameters expected for passerine birds of their size, the Amakihi (L. virens) and the Anianiau (L. parva) range from the expected to the unexpected, respectively (Table 2). L. virens conforms rather closely to the expected passerine patterns with a standard metabolic rate (3.41 cm^3 O_2/g per hr or 6.01 kcal/day) which is 96 per cent of the predicted level (3.55 cm^3 O_2/g per hr or 6.26 kcal/day); with thermal conductance below thermal neutrality which is 99 and 112 per cent of the expected levels at T_A = 9.9 and 20.4°C, respectively; and with rates of evaporative water loss which at T_A = 20.3°C is 63 per cent of that predicted (at

TABLE 2. Comparisons of mean observed and expected (for passerine birds) bioenergetic parameters of Loxops virens and L. parva.

Species, T_A in °C, and Body Weight in g.	Standard Metabolism [a] kcal/day Obs.	Expect.	Standard Metabolism [a] cm^3 O_2/g/hr Obs.	Expect.	Thermal Conductance [b] cm^3 O_2/g/hr/°C Obs.	Expect.	Evap. Water Loss g H_2O/day Obs.	Expect.
L. virens								
T_A = 35.0, wt.= 15.3	6.01	6.26	3.41	3.55				
T_A = 9.9, wt.= 18.7					.189	.191		
T_A = 20.4, wt.= 17.9					.220	.196		
T_A = 20.3, wt.= 18.2							1.84	2.93
T_A = 30.1, wt.= 16.2							2.85	2.86
L. parva								
T_A = 32.4, wt.= 7.9	2.93	3.88	3.22	4.26				
T_A = 35.0, wt. = 8.0	2.98	3.91	3.23	4.25				
T_A = 10.4, wt. = 8.8					.302	.281		
T_A = 20.1, wt. = 8.5					.305	.286		
T_A = 20.0, wt. = 8.5							1.08	2.49
T_A = 30.2, wt. = 8.0							1.64	2.46

[a] Calculated from the relationship $M = 129W^{0.724}$ (M in Kcal/day, W in kg) after Lasiewski and Dawson, 1967.

[b] Calculated from the relationship $C = 0.848\ W^{-0.508}$ (C in cm^3 O_2/g/hr/°C, W in g) after Lasiewski et al., 1967.

[c] Calculated from the relationship $E = 1.563W^{0.217}$ (E in g/day, W in g) after Crawford and Lasiewski, 1968; expected E at T_A = 25°C.

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T_A = 25°C) but at T_A = 30.1°C is nearly identical to that predicted at T_A = 25°C. Rather surprising in L. virens is the demonstration that thermal conductance below thermal neutrality is not constant, but is directly related to T_A (Tables 1 and 2). L. parva, however, deviates rather drastically from the patterns predictable for passerine birds of its size; standard metabolic rate at T_A = 32.4 and 35°C is only 76 per cent of the expected; thermal conductance below thermal neutrality is constant, and at T_A = 10.4 and 20.1°C is 108 and 107 per cent of the expected, respectively; and evaporative water loss at T_A = 20.0 and 30.2°C is reduced to 43 and 67 per cent, respectively, of that predicted at T_A = 25°C.

It is not expected to find bioenergetic parameters which differ from predicted levels, since the latter are derived from equations which ignore the variability upon which they were originally based. It was unexpected, however, to find in two sympatric (at least on Kauai), congeneric passerines, even though they are isolated insular species, one which conforms rather closely to expected values and one which deviates rather drastically. Physiological divergence of such magnitude within a single genus would seemingly preclude the possibility of establishing phylogenetic patterns in bioenergetic pheonomena, at least within the drepanidid subfamily Psittirostrinae.

The intrageneric bioenergetic differences between L. virens and L. parva are summarized diagrammatically in Fig. 4. Particularly impressive are the differences in slope of the lines fitted to the values for oxygen consumption below thermal neutrality; when extrapolated to the abcissa (zero metabolism), these lines for L. virens and L. parva intersect the abcissa at T_A of 62.4 and 48.1°C, respectively, indicating that neither bird conforms to the Newtonian model of homeothermy (see Scholander, et al., 1950). That which conforms the

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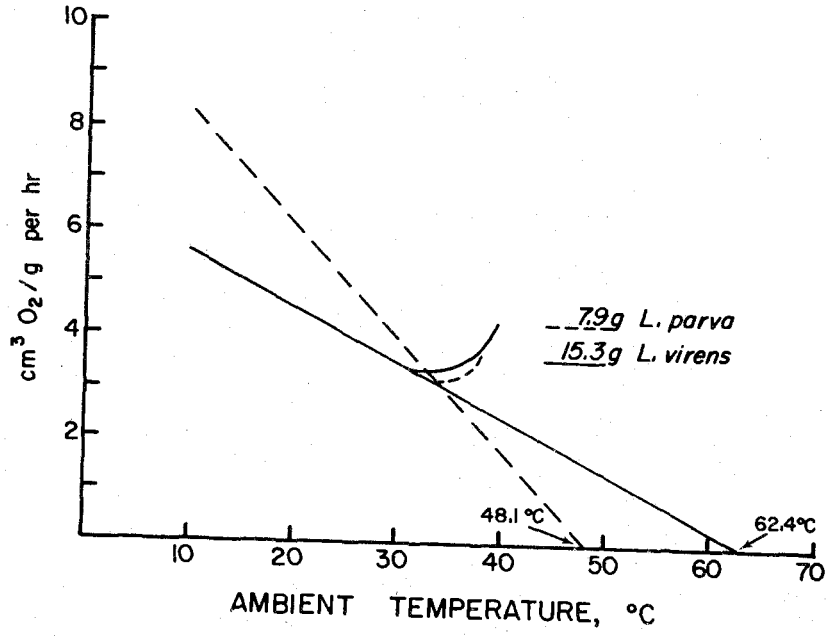

Fig. 4. Summary of the relationship between oxygen consumption and ambient temperature in Loxops virens (solid line) and L. parva (dashed line). The diagonal lines are fitted to the data below thermal neutrality by the method of least squares; the numbers with arrows indicate the temperatures at which these lines, when extrapolated, intersect the abcissa. The lines above the lower critical temperature connect the means measured at the various temperatures. The horizontal lines indicate standard metabolic rates predicted for passerine birds with the mean body weights of L. virens (15.3 g) and L. parva (7.9 g).

least is L. virens, which is to be expected with an inconstant thermal conductance below thermal neutrality (Tables 1 and 2). Such inconstancy of thermal conductance may well be of ecological importance, for nocturnal temperatures in the high forests where these birds live are often below 10°C, and may drop this low in any month of the year (Berger, 1972; Eddinger, 1970); thus under conditions of low T_A and with minimal thermal conductance, energetic costs would also be minimal. The slope of the line relating oxygen consumption to T_A for L. parva is also less steep than might be anticipated (Fig. 4), although thermal conductance was constant at T_A of 10 and 20°C, and higher than predicted for a bird of its size (Table 2). This reduction in slope (and therefore in oxygen consumption at lower T_A) was apparently accomplished by a reduction in T_B at lower T_A; mean T_B at T_A of 10.3°C was 38.3°C, while that at T_A of 20.0°C was 40.0°C (Fig. 1). Thus, both L. virens and L. parva possess differing thermoregulatory capacities which result in energetic savings at lower T_A (10°C), typical of that encountered in their forest habitats at night.

Another striking intrageneric difference between L. virens and L. parva, which is revealed in Fig. 4 and Table 2, is the conformancy to passerine levels of standard metabolism in the former, and the 24 per cent reduction below the expected passerine level in the latter. Thus, although L. parva weighs about 52 per cent as much as L. virens, both have nearly identical energy demands while in thermal neutrality (from T_A of about 31 to 36°C), with that of the former (3.2 cm^3 O_2/g per hr) actually slightly lower than that of the latter (3.4 cm^3 O_2/g per hr).

The most surprising bioenergetic capacity (or incapacity) found in the Honeycreepers was the apparent complete lack of tolerance to high T_A in L. virens, and its inability to control T_B, even at only moderately high T_A, below

lethal levels. Four of six L. virens which had been exposed to T_A between 38.9 and 40.4°C for 1½ hr perished within 36 hr after exposure; this T_A range was equal to or lower than the usual T_B at cooler temperatures. Moderate hyperthermia (mean T_B of 42.9, range 42.2 to 43.6°C) occurred, but T_B never reached 44°C, which is readily tolerated by other passerines (Lasiewski, et al., 1966; Dawson and Hudson, 1970). Lasiewski, et al. (op. cit.) caution investigators to employ high flow rates (and low atmospheric humidities) in respirometry at high T_A, for otherwise, the high atmospheric humidities resulting within the respirometer chambers preclude sufficient evaporative cooling for heat dissipation. At the flow rate employed in this study (800 cm^3/min) and at the T_A ($\bar{X}$ of 39.4°C) which proved lethal, the mean atmospheric humidity (15 per cent rh or 7.8 mm Hg, Table 1) was well within or below the range at which the passerines cited by Lasiewski, et al., (op. cit.) were able to dissipate by evaporative cooling all of the heat produced metabolically. At the mean T_A (39.4°C) which proved fatal to four of six L. virens, only 59.2 per cent of the heat produced metabolically was dissipated by evaporative cooling (Table 1). Thus, it would appear that not only does L. virens lack the tolerances to T_B of ca. 44°C characteristic of most passerines, but also it lacks the apparent avian characteristic (Lasiewski, et al., op. cit.) of dissipating metabolic heat through evaporative cooling under conditions of high T_A and low atmospheric humidity. The absence of this characteristic is not altogether surprising, however, for the highest T_A recorded in the four year period 1966-69 at or near the collecting localities on Kauai and Hawaii are 26.7 and 31.1°C, respectively (Berger, 1972; Eddinger, 1970). Thus, it is doubtful that ambient temperatures for these high forest birds, even though they occur within the tropics, ever exceed thermal neutrality. One can but speculate whether these absences of heat tolerances and

heat dissipating mechanisms are primitive or derived characteristics, but they are certainly atypical of the usual avian condition.

Since great care was taken to avoid lethal temperatures with L. parva, nothing substantive can be said about its high temperature tolerance, except there is no reason to believe, either physiologically or ecologically, that it would differ from that of L. virens.

SUMMARY

Bioenergetically the congeneric Hawaiian honeycreepers Loxops virens and L. parva are quite distinct from each other. L. virens has a higher T_B, lower and inconstant thermal conductance, and a standard metabolic rate (3.41 cm^3 O_2/g per hr) that is 96 per cent of that predicted for passerines. In L. parva, only about half the size of L. virens, standard metabolism (3.22 cm^3 O_2/g per hr) is lower than in the latter, and is reduced to 76 per cent of the predicted passerine level. Neither bird conforms to the Newtonian model of homeothermy, as L. virens has an inconstant thermal conductance below thermal neutrality, while in L. parva thermal conductance is constant but T_B is reduced at low T_A.

Evaporative water loss is rather comparable in both species, conforming closely to expected passerine levels in L. virens but considerably reduced below these levels in L. parva. Under conditions of high T_A, both species become hyperthermic and increase evaporative water loss, but insufficiently to dissipate by evaporation the heat that is produced metabolically, even under conditions of low atmospheric humidity. In four of six L. virens, T_A of ca. 39-40°C and T_B of 42.5-43.6°C proved fatal; L. parva was not exposed to such high T_A. High temperature tolerances apparently are lacking in these species, but they inhabit high forests where such temperatures are seldom encountered.

ACKNOWLEDGEMENTS

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